

## PROJECT DESCRIPTION

Predation is a powerful factor driving the evolution of prey behavior through direct and indirect effects (Lima 1998, 2002, Sih et al. 1998, Abrams 2000, Creel & Christianson 2007). Predators and prey use their sensory systems to detect each other early and enhance prey capture and predator avoidance, respectively (Endler 1991). The current paradigm argues that the sensory systems of predators and prey are asymmetric (Cronin 2005): the predator's sensory system is usually adapted for high performance in specific directions (e.g., high acuity foveae in raptors, Reymond 1987), whereas the prey's sensory system is adapted for detection from any direction (e.g., large visual fields in mallards, Martin 1986a).

To enhance the chances of detecting a predator, prey allocate time to scan their surroundings (antipredator vigilance) while engaged in other tasks (e.g., foraging). During vigilance, prey use their sensory systems to obtain information on cues related to the presence of predators. However, the quality of this information can be 'biased' due to the specialization of the sensory system for other tasks (Endler 1992, Fuller et al. 2005, Mappes & Stevens 2010), such as foraging in micro-habitats with particular visual conditions (e.g., Temple et al. 2010). Consequently, a particular configuration of the sensory system can 'bias' the perception of some types of information under certain environmental conditions, which may prevent prey from detecting predators with equal likelihood in different micro-habitats (Whittingham et al. 2004, Devereux et al. 2006). This information deficit requires prey to gather extra information about the predator (e.g., visually tracking the behavior of the predator) before deciding whether the risk of predation is high enough to escape and how to escape (Ydenberg & Dill 1986, Cooper & Frederick 2007, Cooper 2008, Cresswell et al. 2009). Consequently, gathering information in the early stage of a predator-prey interaction is relevant for prey to avoid engaging in costly escape strategies in response to a predator that might not attack (Hemmi & Zeil 2005).

Antipredator behavior theory predicts that an increase in the risk of predation will enhance vigilance efforts (Lima 1990, Bednekoff & Lima 1998, Caro 2005, Lima & Steury 2005). However, this theory does not consider *how* prey gather information about predators (Fernández-Juricic et al. 2004a). For instance, a common assumption is that prey gather all available information when in vigilance postures (e.g., prey can detect a predator as soon as it breaks cover, prey can gather high quality information 360° around their heads, etc.). Unfortunately, these theoretical assumptions do not reflect the complexity and diversity of the prey sensory systems (Dangles et al. 2009) and vigilance behaviors (Beauchamp 2010, Fernández-Juricic et al. 2010, 2011). Most importantly, antipredator theory does not consider the relationship between the configuration of the sensory system and vigilance behavior (Fernández-Juricic et al. 2004a). This creates a gap in our ability to make predictions about prey responses to predators, limiting the empirical tests of many models. This gap is relevant because adding sensory realism to prey behavior changes the predictions of vigilance and predator detection models (e.g., Fernández-Juricic et al. 2004b).

If we are to fully understand the evolutionary ecology of predator-prey interactions, we need to study the relationship between prey sensory systems and vigilance behaviors to make more informed predictions as to how prey perceive risk through their own sensory cues and how prey respond to predators in different ecological scenarios (Fernández-Juricic et al. 2004a, Hemmi & Zeil 2005). Visually oriented organisms, like birds, are excellent study species because of their complex visual systems (Meyer 1977, Cuthill 2006, Martin & Osorio 2005) and diverse antipredator strategies (Lima 1993, Caro 2005).

I propose to study how vision works in behavioral predator-prey interactions. The *overall goal* of this project is to establish how the configuration of the visual system shapes antipredator behavioral strategies in species that specialize in foraging in micro-habitats (open vs. closed) with different visual challenges. This proposal uses a combination of visual physiology and behavioral ecology approaches to evaluate the independent and combined roles of four visual properties (degree of retinal specialization, motion detection, visual acuity, and size of the blind area) in accounting for antipredator behavior (scanning, predator detection, visual tracking of predators). I will be able to identify how habitat type may have

driven the evolution of visual morphology, and ultimately of antipredator strategies. The findings of this project will allow for the development of a novel sensory framework to gain a deeper understanding of predator-prey interactions based on the prey's visual perception of risk.

**Results from previous NSF support.** NSF award IOS-0641550/0937187 - Broadening Participation Program (from April 2007 to March 2011 with no cost-extensions; \$164,995): 'Effects of the trade-off between visual acuity and visual fields on antipredator behavior in social foraging birds'. PI: Esteban Fernández-Juricic. Fourteen publications (published, in review, to be submitted) have been produced so far. The main conclusions are: (a) distance to a predator and ambient light conditions play a key role in the probability of predator detection (Tisdale & Fernández-Juricic 2009, Fernández-Juricic et al. in rev.); (b) visual acuity explains part of the between-species variability in the detection of cues associated with predators through personal and social information (Tisdale & Fernández-Juricic 2009, Fernández-Juricic & Kowalski 2011); (c) there is a high degree of inter-specific variability in the avian visual system in terms of the morphology of the retina and the configuration of the visual field (Fernández-Juricic et al. 2008, Blackwell et al. 2009, Dolan & Fernández-Juricic 2010, Gall & Fernández-Juricic 2010, O'Rourke et al. 2010a); and (d) inter-specific differences in scanning behavior in birds are based on variations in head movement behavior (Fernández-Juricic et al. 2010, O'Rourke et al. 2010b, Fernández-Juricic in rev. Moore & Fernández-Juricic in rev.). We also developed techniques to measure various properties of the visual system that can be applied across vertebrates (Rogers et al. 2008, Ullmann et al. in rev.).

**Response to a previous review.** This is a resubmission of proposal no. 1121955 (submitted in Jan. 2011). I do appreciate the constructive comments of the Panel and Reviewers as well as the encouragement to resubmit this proposal, which was recommended as high-priority for funding. The Panel summarized the weaknesses and strengths as follows: "The only potential concern was that the choice of species may not give as much information as 20 species chosen more strategically to highlight different habitats across phylogenetic groups. Otherwise, the panel was highly enthusiastic about this potentially transformative project. The panel was confident that the concern could be easily addressed". Instead of proposing 20 species with several pairs within a given Family, the panel recommended choosing "12 species in six pairs". In this new version of the proposal, I not only reduced the number of species but also selected one pair of species (foraging in open- and closed-microhabitats) per Family, following the Panel's suggestion. I chose 14 species in seven Families to keep the minimum sample size required for the statistical analyses. The Panel also noted that "...morphology and vigilance are predicted to vary not just together, but also based on whether species evolved in closed or open habitats". I fully agree with the Panel, and I reflected this by including in the path analysis (Aim #4) habitat type as *the* exogenous predictor variable, which means that habitat type is the factor driving the visual-behavior relationships studied. Finally, the Panel acknowledged that "there are technological advances that still need to be developed but this did not dampen enthusiasm". Although the eye-tracker has not been built yet (which requires the funds requested in this proposal), a representative of Positive Science LLC visited my lab to run some key preliminary tests to determine whether tracking two eyes of a small bird simultaneously would be feasible from a technological standpoint. The good news is that he established that the hardware and software this company already uses will be able to get the job done. Finally, I chose species within driving distance following the suggestion of one of the Reviewers.

### **Avian visual sensory properties associated with antipredator behavior**

In predator-prey encounters, prey follow a sequence of events that enhances the chances of surviving an attack: (1) scan the environment through *visual search* (i.e., no predator around), (2) *detect* the predator, (3) identify and *track* the predator right after detection, and (4) change behavior to reduce visibility and/or escape (Lima & Dill 1990, Caro 2005, Cronin 2005). This proposal focuses on the early stages of the encounter (1-3), when prey must gather visual information in a short period of time to make decisions about the strategies to avoid predation (Hemmi & Zeil 2005). This information could be of a single type (e.g., motion) or multiple types (e.g., resolution, motion, achromatic contrast). Antipredator behavior

theory does not explicitly consider these *multiple* sources of sensory information, which are generally associated with specific properties of the sensory system.

There are different peripheral visual sensory properties that have been implicated in predator detection in birds: (1) degree of retinal specialization, (2) density and distribution of cells associated with motion detection, (3) visual acuity, and (4) size of the blind area at the rear of the bird's head. I will briefly introduce each of these visual properties that determine a large degree of the information that the avian visual system can gather at any given eye and head position.

Birds have a certain degree of visual coverage in their lateral visual fields given by the lateral placement of their eyes in the skull (Fig. 1). The quality of information gathered varies across the retina, because the distribution of photoreceptors (involved in photon capture) and retinal ganglion cells (involved in the transmission of information from the retina to the brain) is not homogeneous (e.g., Querubin et al. 2009). Within the retina, most of the information will be of low quality (low visual resolution) with the exception of a small area of the visual field exposed to the *retinal specialization* (e.g., fovea, area centralis, visual streak; Meyer 1977). The retinal specialization is a spot in the retina with high density of photoreceptors/ganglion cells that provides high quality information (i.e., high visual resolution; Fig. 1; Walls 1942, Meyer 1977). Although bird species vary in the type, number, and position of retinal specializations (Meyer 1977, Collin 1999), in this proposal, I will focus only on species with a single centrally located *fovea* projecting into the lateral visual field (Fig. 1). Species with this type of retinal specialization detect predators and track their position and speed with high accuracy using their lateral visual fields (e.g., Devereux et al. 2006).

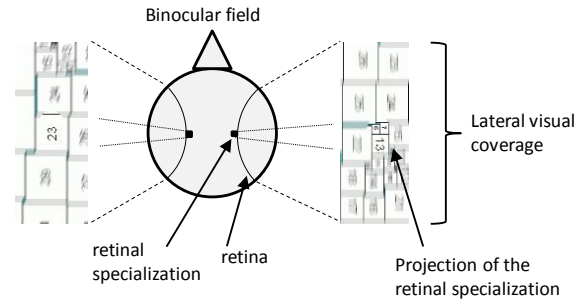


Fig. 1: Schematic representation of the projection of a central retinal specialization (fovea) into the two lateral visual fields at a given head and eye position (projection of the binocular field not shown for clarity). The figures with numbers represent the visual scenes perceived by each eye. Visual resolution is the highest at the retinal specialization, but decreases towards the retinal periphery (e.g., blurred vision) due to lower density of photoreceptors and retinal ganglion cells.

Besides the local increase in visual resolution, the fovea is thought to reduce light scattering (Martin 1986b), facilitate image magnification (Walls 1942), aid in image fixation and exaggeration of small movements (Pumphrey 1948), and provide directional focus (Harkness & Bennet-Clark 1978). Snyder & Miller (1978) demonstrated that the depth of the fovea can influence the degree of visual resolution *within* the retinal specialization. At the very center of the fovea, the ganglion cell, inner plexiform, and nuclear retinal layers may be displaced radially, giving rise to tissue invagination and a pit in the retina (Fig. 2, Pumphrey 1948, Meyer 1977, Ruggeri et al. 2010). The depth of the foveal pit varies between two extremes. Concaviclivate foveae have a shallow pit, whereas convexiclivate foveae have a deep and funnel-shaped pit (Fig. 2; Walls 1937, Pumphrey 1948). Given similar density of photoreceptors or retinal ganglion cells, deep foveae can enhance the visual resolution *within* the retinal specialization by increasing the focal length of the eye in relation to shallow fovea (Snyder & Miller 1978).

Therefore, *deeper foveae are considered to have a greater degree of retinal specialization than shallower foveae* (Walls 1937, Harkness & Bennet-Clark 1978).

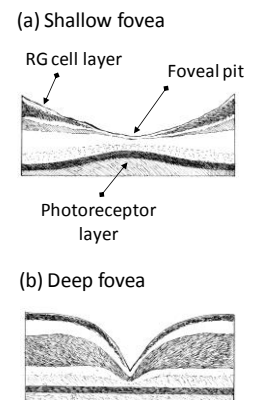


Fig. 2: Cross section of the fovea, showing foveal pits of different depth: (a) shallow, and (b) deep.

Two other visual properties at the retinal level relevant to detecting predators are the ability to sense motion and changes in achromatic contrast (i.e., visual targets varying in light intensity but not in spectral composition) in a scene (Cronin 2005). Prey benefit by having a visual system with high sensitivity to stimuli moving against the background that can be discriminated in the early stages of visual processing (Levin 1997, Jablonski & Strausfeld 2000). Detecting motion through motion sensitive neurons allows individuals to estimate the time remaining before collision (Rind & Simmons 1999, Xiao et al. 2006) based on a hierarchical system of cues that includes changes in the rate of increase in size and complexity

of the moving object (Carlile et al. 2006). Motion detection is mainly an achromatic visual task, along with the detection of the location and shape of objects in a visual scene (Osorio et al. 1999, Burton 2000, Dittrich & Lea 2001).

The detection of motion and light intensity in the avian retina has been associated with a type of photoreceptor called *double cone* through both physiological (von Campenhausen & Kirschfeld 1998) and behavioral (Goldsmith & Butler 2005) studies. Double cones have principal and accessory members with broad spectral sensitivity (Bowmaker et al. 1997, Osorio & Vorobyev 2005, Hart & Hunt 2007). Double cones can be quite abundant in the avian retina (25-50% of all cones), and interspecific variations in their *density* and *distribution* can be proxies of the ability to detect changes in motion and achromatic contrast, such as those associated with predator attacks (Hart 2001).

Another visual property involved in predator detection is the overall visual acuity of the eye, which is the ability to resolve fine details, such as distinguishing between two closely-spaced stimuli (McIlwain 1996). For prey, variation in visual acuity can have implications for the distance at which an attacking predator is detected and recognized (Tisdale & Fernández-Juricic 2009). Larger eyes project a larger image on the retina, thereby increasing the resolution of objects because the image is spread over a larger number of photoreceptors that transfer the information to the retinal ganglion cells (Land & Nilsson 2002). Evidence shows that larger bird species have larger eyes (Howland et al. 2004, Burton 2008), and thus higher overall visual acuity (Kiltie 2000). Furthermore, visual acuity increases as the density of photoreceptors and ganglion cells increases across the whole retina (Land & Nilsson 2002). Other factors can influence visual acuity (corneal diameter, aberration, diffraction, light intensity, etc.); however, they will not be considered in this proposal, as I will focus on diurnal birds, which are not limited by sensitivity to ambient light and have approximately similar eye shapes (Martin 1993, Hall & Ross 2006).

Finally, the position of eyes in the skull can influence the amount of visual coverage around the head (e.g., Heesy 2008), and thus the size of the blind area at the rear of the head (Martin 2007). Species with more frontally placed eyes will have wider blind areas, and less visual coverage at any given head position (Iwaniuk et al. 2008). Given the short time windows for prey to escape, species with wider blind areas allocate more time to vigilance behavior probably to compensate for the lack of visual coverage (Guillemain et al. 2002). Moreover, predator detection is delayed when the attacker's approach is in the prey's blind area rather than in either lateral visual field (Kaby and Lind 2003, Devereux et al. 2006).

How these four visual properties affect each other, and most importantly how they influence antipredator behavior, has yet to be studied. These visual properties are likely to interact to gather information about predators through scanning behavior. This project takes a mechanistic view of scanning behavior as changes in eye and head positions to gather visual information (Lemeignan et al. 1992, Dawkins & Woodington 2000, Dawkins 2002, Moinard et al. 2005, Jones et al. 2007a). Birds change the orientation of their eyes and heads quickly (a) to vary the position of the retina and increase visual coverage around the visual space limited by the blind area (Fig. 1; Dunlap and Mowrer 1930, Friedman 1975, Fernández-Juricic et al. 2010), and (b) to expose the fovea to objects of interest in the environment and gain high quality information (Fig. 1; Bloch et al. 1984, Maldonado et al. 1988). Head movements in birds are more frequent and of greater amplitude than eye movements (Gioanni 1988, Haque & Dickman 2005), since the eye fits tightly in the orbit, limiting its movement to a certain degree (Jones et al. 2007b). However, it is necessary to consider the role of eye movements in information gathering because they can change the size of the blind areas (e.g., by diverging the eyes) in some species, thereby affecting visual coverage (Fernández-Juricic et al. 2008, 2010).

Scanning behavior and predator detection have been shown to vary with different habitat characteristics (e.g., Carrascal et al. 2001, Whittingham et al. 2004, Cooper & Whiting 2007, Fernández-Juricic & Tran 2007, Gall & Fernández-Juricic 2009). This is likely related to changes in ambient light conditions and

vegetation complexity in different habitat types (Endler 1993, Denno et al. 2005, Théry 2006). Consequently, we can expect variability in the way different species perform visually through variations in the signal-to-noise ratio as a function of habitat type and visual system properties (Stevens 2010). There is certainly a high degree of interspecific variability in avian visual properties (retinal specialization, Meyer 1977, Collin 1999; density and distribution of double cones, Hart 2001; visual acuity, Kiltie 2000; size of the blind areas, Martin 2007) in species living in different habitats. There is also interspecific variability in the amplitude and rates of eye and head movements that control scanning behavior (Wallman & Pettigrew 1985, Wallman et al. 1994, Casperson 1999, O'Rourke et al. 2010a-b, Fernández-Juricic et al. 2010). This proposal will be the first attempt to explain the variation in avian vision and scanning behavior in species specialized in foraging in more open and more closed habitats through a comparative study.

### Hypotheses, predictions, and preliminary information

The *specific goal* of this project is to establish how different visual properties shape avian scanning behavior that enhances the chances of detecting and visually tracking predators in visual conditions simulating different habitat types (i.e., open vs. closed). Two general hypotheses are considered.

The **first hypothesis** is that the degree of retinal specialization, motion detection, visual acuity, and size of the blind area will affect scanning behavior and predator detection in different ways (see details below) leading to *different strategies of gathering visual information* about predators. I expect that the degree of retinal specialization will influence the three stages of information gathering (visual search, predator detection, visual tracking of predators), whereas motion detection, visual acuity, and the size of the blind area will affect the first two stages (visual search, predator detection). The following paragraphs describe the expected effects of each visual property on these stages.

Deep foveae have greater optical power compared to shallow foveae (see above). However, there are some disadvantages associated with the presence of a deep fovea that are expected to affect scanning behavior. First, the *deeper* the foveal pit, the *narrower the width* of the foveal pit (Fig. 2, Fite & Rosenfield-Wessels 1975), and thus the smaller the area with the highest visual resolution in the visual field (Fig. 3). Second, species with a deeper fovea can have a steeper decline in retinal ganglion cell density (and thus visual resolution) from the fovea towards the periphery of the retina compared to species with a shallower fovea (Fig. 3). I have preliminary information from 17 bird species with foveae showing that ganglion cell density in the fovea was positively and significantly correlated with the slopes of change in cell density in the nasal ( $r = 0.90$ ,  $P < 0.001$ ), temporal ( $r = 0.81$ ,  $P < 0.001$ ), dorsal ( $r = 0.61$ ,  $P = 0.009$ ), and ventral ( $r = 0.86$ ,  $P < 0.001$ ) sides of the retina (figures available at:

<http://estebanfj.bio.purdue.edu/vis&vig.html>). Therefore, two trade-offs are expected in terms of the degree of retinal specializations: species with a deeper fovea are expected to have higher visual resolution *within* the fovea, but (1) a reduced

proportion of their visual field with the highest visual resolution as well as (2) a greater difference in visual resolution from the fovea to the retinal periphery (Fig. 3). Variations in the degree of visual resolution within the retinal specialization and between the retinal specialization and the retinal periphery can affect scanning behavior (Whiteside 1967).

In a visual search context, I predict that as the degree of retinal specialization increases (i.e., deeper

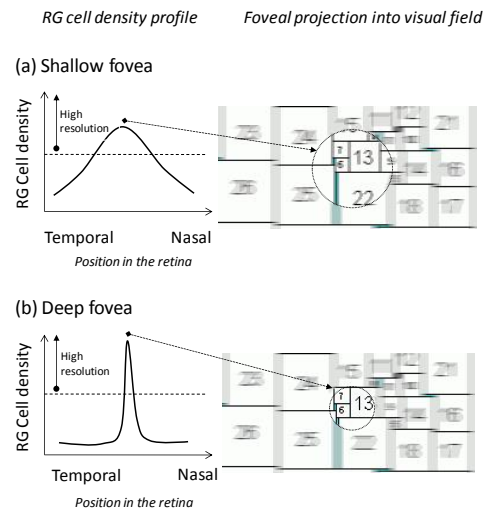


Fig. 3: Each fovea type (a, shallow; b, deep) is proposed to have a different profile of the variation in retinal ganglion cell density (RC density) from the fovea to the periphery of the retina (shown here is the temporal-nasal axis). Shallow foveae are expected to have relatively lower visual resolution, but a less steep reduction in cell density towards the retinal periphery, leading to a larger proportion of the visual field with high resolution. Deep foveae are expected to have relatively higher resolution, but a steeper reduction in cell density towards the retinal periphery, leading to a smaller proportion of the visual field with high resolution.

foveae), eye and head movement rates will increase to enhance visual coverage with the high resolution of the fovea based on the aforementioned trade-offs. Given similar rates of eye/head movements, I predict that species with deeper foveae will have lower chances of detecting a predator than species with shallower fovea due to the relatively lower proportion of the visual field with the high visual resolution and the greater difference in resolution between the fovea and the retinal periphery (Fig. 3). In a visual tracking context, I predict that as the degree of retinal specialization increases (i.e., deeper foveae), the time spent with the head orientation that aligns the fovea with an object of interest will increase to take advantage of the image enhancement benefits within the fovea. We have evidence supporting some of these predictions. In a comparison between two bird species belonging to the Emberizidae Family, we found that the species with a steeper decline in ganglion cell density (and thus steeper decline in visual resolution) from the fovea towards the retinal periphery showed higher head movement rates compared to the species with a less steep decline in ganglion cell density (Fernández-Juricic et al. 2011a). Additionally, using an optical method to estimate the depth of the foveal pit, we found preliminary evidence showing that species with deeper foveae have larger degrees of eye movement ( $r = 0.52$ ,  $P = 0.033$ ,  $n = 17$  Passeriformes). We also found that species with a large degree of eye movement show high head movement rates ( $r = 0.85$ ,  $P = 0.002$ ,  $n = 10$  Passeriformes). It is important to note that the depth of the foveal pit is a proxy of visual resolution *within* the fovea, but not necessarily a proxy of the overall visual acuity of the eye. We actually found that there was no significant correlation between (log) eye size (a proxy of visual acuity of the eye) and the depth of the foveal pit ( $r = -0.12$ ,  $P = 0.685$ ,  $n = 17$  Passeriformes).

The density and distribution of double cones is expected to influence the ability of prey to detect predators (Hart 2001), given their role in motion detection and achromatic contrast (von Campenhausen & Kirschfeld 1998; Goldsmith & Butler 2005). I predict that in a visual search context, bird species with double cones concentrated on one sector of the retina will have higher eye/head movement rates to expose the motion detection sector to as many different spots in the visual space as possible compared to species with a less spatially restricted distribution of double cones. Moreover, species with a more spatially restricted distribution of double cones are expected to have a lower probability of detecting predators from any direction because a relatively lower proportion of the visual field will have a high density of motion detectors. Given similar rates of eye/head movements, I predict that species with proportionally higher density of double cones in relation to other photoreceptor types will have higher probabilities of detecting predators than those species with a proportionally lower density of double cones. We have evidence showing that the density of double cones increases the probabilities of detection. We found that mourning doves ( $55.88 \pm 0.44/\text{mm}^2$ ) had a higher density of double cones than brown-headed cowbirds ( $29.04 \pm 0.45/\text{mm}^2$ ; Ojeda & Fernández-Juricic, unpublished ms), and that mourning doves reacted to the approach of a rapidly moving object significantly earlier than brown-headed cowbirds (Blackwell et al. 2009).

Visual acuity can play an important role in antipredator behavior, as species with higher overall visual acuity (e.g., larger eyes) will be able to resolve objects to a greater extent than species with lower visual acuity. Given similar degrees of retinal specialization, species with higher overall visual acuity are expected to have lower eye/head movement rates than those with low acuity in a visual search context, because at a given distance they can resolve objects to a greater degree across their visual field. On the other hand, species with lower overall visual acuity are expected to have higher eye/head movement rates to update the status of their visual surroundings more quickly and check for the presence of threats. Given similar degrees of retinal specialization, I also predict that species with higher overall visual acuity will have a higher probability of predator detection than those with lower visual acuity because they can resolve objects from farther away. There is evidence showing that birds with larger eyes detect threats and predators earlier than those with smaller eyes (Blumstein et al. 2005, Tisdale & Fernández-Juricic 2009).

The size of the blind area at the rear of the animal's head will limit the area covered by the visual field. Species with wider blind areas are expected to have higher eye/head movement rates than species with narrower blind areas to compensate for the lack of visual information. Furthermore, species with wider

blind areas are expected to have lower probabilities of predator detection than species with narrower blind areas due to the larger blind spot present at any given eye/head position. There is evidence showing that species with larger blind areas increase the amount of time spent vigilant (Guillemain et al. 2002, Tisdale & Fernández-Juricic 2009).

These four visual properties have been studied separately in the past; thus, I presented predictions on their *independent* effects on the different stages of information gathering. Nevertheless, the findings of this study will provide the opportunity to assess *associations* between visual properties (e.g., potential sensory trade-offs) as well as their *combined* effects on antipredator behavior.

The **second hypothesis** is that the relative importance of the four visual properties studied (degree of retinal specialization, motion detection, visual acuity, size of the blind area) in terms of predator detection will vary depending on the visual conditions of the species' foraging micro-habitat (i.e., open vs. closed). This hypothesis is focused on *aerial predation*, which is an important source of lethal and non-lethal effects on adult birds (Cresswell & Whitfield 1994, Owens & Bennett 1994, Lima 1998, Caro 2005, Roth et al. 2005, 2006, Roth & Lima 2007). Predators are known to change their attack strategies in relation to vegetation complexity (e.g., Denno et al. 2005, Michel & Adams 2009), and therefore prey are exposed to predators to a different degree depending on the level of visual obstruction in the environment, which ultimately can affect scanning behavior (Gall & Fernández-Juricic 2009). Species specialized in foraging in more closed habitats will be limited mostly by *visual coverage* to detect predators from any direction (e.g., above, below), as the high degree of vegetation complexity will bring predators and prey spatially closer before an attack (i.e., shorter predator exposure times). Consequently, these species are expected to have relatively narrow blind areas, a large proportion of the visual field with high visual resolution (lower degree of retinal specialization, Fig. 3), and more homogeneous distribution of double cones, which can increase the probabilities of predator detection from different directions in complex visual environments. Species specialized in foraging in more open habitats will be limited mostly by *visual acuity*, which will influence the distance at which prey can resolve predators, as the low degree of vegetation complexity will place predators farther from prey (i.e., longer predator exposure times) and limit the direction from which most attacks can be expected (e.g., above the ground). Consequently, these species are expected to have high overall visual acuity, high degree of retinal specialization, and a more localized distribution of double cones, which can increase the probabilities of predator detection from the specific directions of the visual field (e.g., above the ground) where aerial predator attacks are more likely. There is evidence showing that bird species living in open habitats have larger eyes and thus higher visual acuity than species living in more complex habitats (Møller & Erritzøe 2010).

## Research plan

The project is designed with four specific aims. I will first determine the degree of inter-specific variability in the degree of retinal specialization, motion detection, visual acuity, and size of the blind area (Aim 1). I will then establish the degree of inter-specific variability in three visual tasks associated with gathering information about predators (visual search, predator detection, visual tracking of predators) under highly-controlled conditions (Aim 2) and ecologically-relevant conditions (Aim 3). Finally, the species-specific information collected in Aims 1-3 will be used in Aim 4 to assess the relationships between vision and behavior under visual conditions simulating open and closed habitats using a structural equation modeling approach. I provide brief descriptions of the physiological and behavioral techniques to be used, cite papers that describe further methodological details, and refer to online media materials.

**Table 1:** Study species with equal numbers from each type of foraging microhabitat (open, closed) within each of seven Families of Passeriformes. There are no significant differences in body mass between open- and closed-habitat species ( $F_{1,12} = 0.45, P = 0.513$ ).

Scientific name	Common name	Foraging microhabitat
<b>Family Corvidae</b>		
<i>Pica hudsonia</i>	Black-billed Magpie	Open
<i>Cyanocitta cristata</i>	Blue Jay	Closed
<b>Family Emberizidae</b>		
<i>Chondestes grammacus</i>	Lark Sparrow	Open
<i>Passerella iliaca</i>	Fox Sparrow	Closed
<b>Family Icteridae</b>		
<i>Xanthocephalus xanthocephalus</i>	Yellow-headed Blackbird	Open
<i>Icterus galbula</i>	Baltimore Oriole	Closed
<b>Family Fringillidae</b>		
<i>Spinus tristis</i>	American Goldfinch	Open
<i>Acanthis flammea</i>	Common Redpoll	Closed
<b>Family Turdidae</b>		
<i>Sialia sialis</i>	Eastern Bluebird	Open
<i>Hylocichla mustelina</i>	Wood Thrush	Closed
<b>Family Tyrannidae</b>		
<i>Tyrannus tyrannus</i>	Eastern Kingbird	Open
<i>Empidonax virescens</i>	Acadian flycatcher	Closed
<b>Family Parulidae</b>		
<i>Dendroica discolor</i>	Prairie Warbler	Open
<i>Parula americana</i>	Northern Parula	Closed



**Model species:** I will characterize four visual properties and three visual tasks in 14 species of Passeriformes from seven Families: Corvidae, Emberizidae, Icteridae, Fringillidae, Turdidae, Tyrannidae, and Parulidae. I chose Passeriformes because it is the most phylogenetically diverse group of birds with high variability in ecology and morphology (Bennett and Owens 2002, Ricklefs 2003). Within each Family, I chose one pair of open- and closed-habitat species based on the criterion that each spends >50% of the time foraging in either open or closed micro-habitats (Table 1). The selection of species was intended to minimize differences in body mass between habitats (see Table 1) and allow for the capturing of individuals in locations within 12 hours of driving distance. All these species are subject mostly to aerial predation by different raptor species (Birds of North America: <http://bna.birds.cornell.edu/bna/>). I have preliminary evidence from each of these Families showing the presence of a central fovea. Individuals will be captured using a combination of mist nets, Australian traps, and walk-in traps in different states. My lab has experience catching and handling species from all these Families. We will also be assisted by APHIS personnel (USDA), with whom we currently collaborate. Individuals will be ground-transported, and kept at Purdue Animal Facilities. I am confident that the information on 14 species can be obtained within the timeline proposed (see below). For instance, my students and I gathered preliminary information for this proposal by measuring behavioral and physiological parameters on 17 bird species (many of them different from the ones proposed here) over a 1.5 year period.

**Aim 1: To establish the degree of inter-specific variability in the four visual properties that are expected to affect antipredator behavior: degree of retinal specialization, motion detection, visual acuity, and size of the blind area.** This aim will provide the necessary information on the visual systems of 14 species of Passeriformes to establish vision-behavior relationships in the context of predator detection in Aim 4. My lab has the necessary expertise, techniques, and equipment to characterize all these visual properties implemented as a result of a previous NSF award (IOS-0641550/0937187).

I will measure three elements of the degree of retinal specialization: gradient of change in retinal ganglion cell density from the fovea to the retinal periphery (Fig. 3) and width and length of the foveal pit (Fig. 2). Eight individuals of each species (4 from each sex, with 2 right and 2 left retinas from each sex) will be used. I will employ a retinal wholemount technique to remove, fix, and stain the retinal ganglion cell layer (Stone 1981, Ullmann et al. in rev.). Stained retinal ganglion cells will be examined under an Olympus BX51 microscope at x100 power. I will trace the perimeter of the retina using StereoInvestigator 9.13 (MBF Bioscience), and then overlay a grid with 250 sampling sites (50 $\mu$ m x 50  $\mu$ m) to photograph the retinal ganglion cell layer, and count the cells with ImageJ (<http://rsbweb.nih.gov/ij/>) to estimate density (number of cells per mm<sup>2</sup>). I will build topographic maps (following Stone 1981), which reflect variations in the density of retinal ganglion cells across the retina (e.g., Fernández-Juricic et al. 2011b; examples available at: <http://estebanfj.bio.purdue.edu/vis&vig.html>). Based on the topographic maps, I will overlay two sampling lines (nasal-temporal and dorsal-ventral) centered on the fovea, estimate cell density at equally-spaced points along the lines, and calculate the slope of change in cell density from the fovea to the retinal periphery (Moore et al. to be submitted July 2011). I will obtain averaged slope values per individual and per species. To measure the foveal pit parameters, I will conduct *in vivo* noninvasive imaging of the retinal tissue with an interferometer-based imaging technique (OCT, Tanna et al. 2010). This technique has been used successfully in birds (Ruggeri et al. 2010), and the high resolution imaging allows for the quantification of the width and depth of the foveal pit (Dubis et al. 2009, Chalam et al. 2010). We have already contacted a veterinary ophthalmologist who is willing to help us obtain the OCT scans. I will use a principal component analysis to summarize the three parameters (slope of cell density gradient from the fovea to the retinal periphery, depth of foveal pit, width of foveal pit) into a single component called degree of retinal specialization.

I will estimate the density and distribution of double cones based on oil droplets. Each avian cone type has an oil droplet associated with it, which filters light before reaching the visual pigment (Hart & Hunt 2007). The oil droplet associated with the double cone is the P-type (principal) (Jane and Bowmaker 1988;



Bowmaker et al. 1997). Different oil droplets (and thus cones) can be discriminated in fresh retinas using a combination of bright and fluorescent lights (see criteria in Hart 2001). I will use the remaining retinas from the same 8 individuals per species used for the retinal ganglion cells (4 males and 4 females, with 2 right and 2 left retinas per sex). I will extract the retina, flatten it, place it in phosphate-buffered saline solution, and cover slip it. Density and distribution of double cones will be measured using the same microscope, software, and mapping procedures described above. I will obtain averaged double cone density values per individual and per species based on the highest 25 percentile oil droplet density (Dolan & Fernández-Juricic 2010). I will develop topographic maps of P-type oil droplet density across the retina of each individual. Based on the topographic maps, I will determine the degree to which the distribution of double cones is spatially restricted or homogeneous. First, I will overlay two sampling lines (dorsal-ventral, frontal-temporal) on a topographic map centered on the fovea. Second, I will estimate the relative length that each isodensity area occupies along these two sampling lines. Third, using the length and P-type oil droplet density values obtained from the sampling lines, I will estimate the length of the mean vector ( $r$ ) in Oriana 3 ([www.rockware.com](http://www.rockware.com)), which estimates how homogeneous cell densities are distributed among the sampling lines. High  $r$  values indicate that cell density is higher in one direction, whereas low  $r$  values indicate that cell density is evenly distributed in all directions.

I will estimate overall visual acuity anatomically, which correlates well with behavioral estimates of acuity particularly when using peak retinal ganglion cell density values (Pettigrew et al. 1988). I will measure eye size (eye axial length) and estimate averaged retinal ganglion cell density based on the highest 25<sup>th</sup> percentile cell density value per individual from the topographic maps (Dolan & Fernández-Juricic 2010, Fernández-Juricic et al. 2011a). I will first calculate the average posterior nodal distance (PND) as: eye axial length\*0.60 (Martin 1993). I will then calculate the retinal magnification factor (RMF), which is the linear distance on the retina that subtends 1° (Pettigrew et al., 1988) as:  $RMF = (2\pi PND)/360$ . The estimate of visual acuity will be  $F_n$ , the highest spatial frequency that can be detected, which will be calculated following Williams & Coletta (1987) based on RMF and cell density. Averaged visual acuity will be estimated per species.

The size of the blind area will be measured on 8 live individuals per species with an ophthalmoscopic reflex technique (Martin 2007; Fernández-Juricic et al. 2010). Individuals will be restrained at the center of a visual field apparatus (pictures available at: <http://estebanfj.bio.purdue.edu/vis&vig.html>). I will measure the retinal margins of each eye at each elevation in 10° increments using a Keeler Professional ophthalmoscope. Measurements will be done when individuals have their eyes at rest, converged, and diverged following Fernández-Juricic et al. (2008). I will first estimate the size of the cyclopean field as (binocular + lateral right + lateral left visual fields), following (Fernández-Juricic et al. 2008). I will then estimate the size of the blind area as (1 – cyclopean area) at each elevation around the head, and get averaged values per individual across elevations and per species for eyes at rest, converged, and diverged. Separate analyses will be run for each of these three eye position categories in Aim 4.

**Aim 2: To determine the degree of inter-specific variability in eye movement and head movement behaviors under controlled conditions.** This aim will provide information on visual search (e.g., eye and head movements without objects of interest in the visual environment), probabilities of detecting an object, and patterns of eye and head movement behavior while tracking a moving object from 14 different species of Passeriformes. I will manipulate the presence of objects and their movement in a virtual environment (following Voss & Bischof 2009) to identify strategies of information gathering by measuring responses to the same visual stimuli in visual conditions simulating closed (i.e., short exposure time) and open (i.e., long exposure time) habitats. The information will be used in Aim 4 to establish vision-behavior relationships.

I will restrain an individual with a similar system to that used for the visual field measurements described in Aim 1. The individual will be surrounded by three LCD screens with high flicker rate (Sony BRAVIA

32", 1080p, 120Hz, Fig. 4) to minimize bias due to the high avian visual temporal resolution (D'Eath 1998). The center of the lateral screens will coincide with the relative position of the projection of the central fovea. The experimental arena will be surrounded by a black screen to avoid any other visual stimulation (Fig. 4). I will measure eye movements in head-restrained conditions, and head movements in head-free conditions. Characterizing both eye and head movements will provide a better understanding of whether these two mechanisms of information gathering generate similar or different scanning patterns.

In the *head-restrained condition*, individuals will be fitted with an eye tracking device specifically designed for small birds by Positive Science LLC (<http://positivescience.com/>). The apparatus will consist of four miniature cameras. Two infrared eye-cameras will be mounted on adjustable arms approximately 25 mm away from the head of the bird to capture close-up images of both the left and right eyes simultaneously. A dark-pupil illumination technique will allow the software to track the pupil and corneal reflection. Two wide-angle reference scene cameras will be placed just above the bird's head to provide a reference for eye. After calibration, the software will render a new video stream with gaze position superimposed. We have successfully tested a prototype of this system in a small Passeriform (video available at: <http://estebanfj.bio.purdue.edu/vis&vig.html>). We have recorded eye movement patterns of several bird species in head-restrained conditions successfully (without the eye tracker), so I do not foresee major problems with birds adjusting to this experimental scenario.

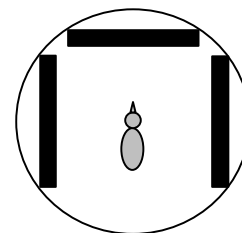


Fig. 4: Schematic representation (not to scale) of the position of the animal in relation to the three LCD screens (one frontal, two lateral). The area will be surrounded by a black screen.

In the *head-free condition*, I will use three camcorders located 60 cm on-top of the animal to record head movements (1 camera) and the objects presented in the lateral LCD screens (2 cameras). A multiplexer and a digital video recording system (Radical HDC-0912) will allow me to record all three cameras on the same screen. Based on the retinal topographic maps and pictures of the position of the eye in the skull of each species (Aim 1), I will estimate the projection of the fovea from a top-view, which will be used to measure changes in head position in relation to the visual stimuli with Graphclick (<http://www.arizona-software.ch/graphclick/>). I will not use an eye tracker for the head-free condition because the technology is not advanced enough to measure movements of both eyes simultaneously when the head moves freely in small birds.

Prior to the experiment, each individual will undergo two habituation sessions per condition. In each condition (head-restrained, head-free), individuals will be exposed to three phases within a single trial (~ 6 min): (1<sup>st</sup>) visual search (no stimuli on the screens), (2<sup>nd</sup>) visual detection of a virtual object, and (3<sup>rd</sup>) visual tracking of a virtual object. In the visual search phase, the LCD screens will be on but covered with white plastic to record eye/head movement rates over 3 mins. In the visual detection phase, I will present a stationary black circle (diameter = 2 degrees of visual angle) in a random position on one of the lateral LCD screens. The circle will be exposed a short (0.5 sec) or long (1 sec) time period, and will be presented in either the right or left lateral screen. Exposure times were chosen to be higher than the minimum frequency of spontaneous eye movement rates with the head restrained (Voss & Bischof 2009). Therefore, there will be four treatments (short exposure left, short exposure right, long exposure left, long exposure right) that will be presented in a randomized order with 15 sec inter-stimulus intervals. I will measure whether individuals detected the stimuli when the deviation of the eye/head is less than 15 degrees from the direction of the stimulus within one sec of exposure (Voss & Bischof 2009). The probability of object detection per species will be estimated with a generalized linear model. In the visual tracking phase, I will present a black circle (diameter = 2 degrees of visual angle) that will move (without changing size) around one of the LCD screens at a speed of 30 degrees per sec for 30 sec following a random walk trajectory. This stimulus will be presented in either the right or left lateral screen. I will score eye/head movement rates and their intervals in response to the stimulus following the aforementioned criteria (Voss & Bischof 2009).

I will use 15 individuals per species. Each individual will be exposed to the head-restrained condition and head-free condition in a random order on different days. All LCD screens will be on during the experiment with a light grey background. Stimuli will only be displayed in the lateral screens as this study focuses on lateral visual fixation (instead of binocular fixation), because it is more relevant for detecting distant stimuli (Maldonado et al. 1988), such as predators. I will measure irradiance and reflectance off the LCD screens at the beginning of each trial to make sure we adjust for any inequality in achromatic and chromatic contrasts across trials. Although I acknowledge that laterality (Rogers 2008), visual attention (Dukas and Kamil 2000), and looming effects (Rind & Simmons 1999) may play a role in lateral visual fixation, the proposed experimental design intends to minimize these potential confounding effects.

**Aim 3: To establish the degree of inter-specific variability in head movement behavior in a predator-prey interaction event under ecologically relevant conditions.** This aim will provide information on visual search, probability of predator detection, and head movement patterns while tracking a predator from 14 different species of Passeriformes. I will manipulate the presence of a model predator in a semi-natural experiment conducted outdoors simulating two visual environments: closed habitat (i.e., short predator exposure) and open habitat (i.e., long predator exposure). This component of the project is important to establish whether the inter-specific variability in the strategies of information gathering identified in Aim 2 apply to a predator-prey interaction context in natural conditions. This information will be used in Aim 4 to establish vision-behavior relationships.

I will conduct this study on a grassy area on campus that is limited by woodland on the east side. I will use a foraging paradigm by which an individual in a circular 1-m<sup>3</sup>-mesh-wire enclosure (with a perching rod) will have a limited amount of food (seeds of different kinds or mealworms, depending on the species) hidden in a sawdust substrate (Fig. 5). For ground foraging species, food will be on the ground; whereas for tree foraging species, food will be in small caps next to the perching rod. As found in previous studies in similar conditions (e.g., Fernández-Juricic et al. 2004c), individuals will search for food and scan for potential threats. Two cameras (1 top-view and 1 lateral-view) attached to a stand holding them at the same position and angle across trials will record the behavior of the individual. The flying path of the predator model will be video-recorded by a camera controlled by a hidden observer and another camera located on top of the subject's enclosure oriented towards the predator exposure area (Fig. 5). Through a multiplexer and a digital video recording system (Radical HDC-0912), all cameras will be recorded on the same screen. The experimental set-up will simulate visual conditions in open and closed habitats. For the closed habitat condition, the enclosure will be covered on top by artificial vegetation and will be surrounded by a series of 1.5-m-high black screens at regular intervals, simulating the type of visual obstructions found in closed habitats but leaving an open area where a predator model will be exposed (Fig. 5a). For the open habitat conditions, the enclosure will not be covered by artificial vegetation on top or be surrounded by any visual screen (Fig. 5b). I successfully conducted studies with this kind of manipulations in semi-natural conditions to simulate open and closed foraging micro-habitats, which resulted in antipredator behavior patterns (Fernández-Juricic & Tran 2007) that mimicked responses recorded from free-ranging birds (Carrascal et al. 2001).

I will use a radio-controlled aircraft with the shape and color of a goshawk (*Accipiter gentilis*) called FALCO Robot GBRS (Bird Raptor International: <http://www.bird-raptor.com/>). My lab currently has two FALCO units that will be used in this experiment. Although powered by a low-noise propeller, the FALCO is designed to glide once it is at the right altitude, with its flying path controlled by a pilot on the ground. Consequently, the FALCO can mimic the behavior of a real predator and cause regular antipredator behavior (video at: <http://estebanfj.bio.purdue.edu/vis&vig.html>). We have already conducted

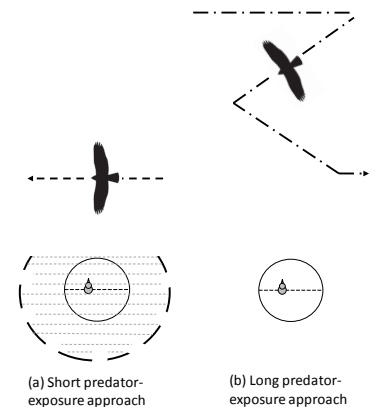


Fig. 5: Schematic representation (not to scale) of the enclosure (with food and a perch) and the area in which the predator model will be exposed to the animal through two types of approaches: (a) short predator exposure, and (b) long predator exposure.

successful tests with the FALCO approaching brown-headed cowbirds.

The FALCO will be flying over the woodland area about 250 m away from the view of the animal *before* the beginning of each trial, and then it will glide towards the test subject (Fig. 5). I will expose two groups of different individuals from each species (12 individuals per group per species) to two combinations of predator approach/visual conditions: (a) short predator exposure in closed habitat conditions, and (b) long predator exposure in open habitat conditions. These two predator exposure times represent two (of many) general attack strategies in closed (short exposure, close distance between predator and prey) and open (long exposure, long distance between predator and prey) habitats, associated with differences in the degree of vegetation complexity. In the short predator exposure approach, the FALCO will appear 20 m away from the enclosure, fly parallel to the enclosure close to the ground and return to the woodland area (Fig. 5a). In the long predator exposure approach, the FALCO will appear in the exposed portion of the experimental set-up 100 m away from the enclosure, fly diagonally close to the ground until it is 20 m away from the enclosure where it will divert back to the woodland area (Fig. 5b). Predator speed will be checked with an onboard GPS logger and maintained similar in both approaches. Each individual will be exposed to the FALCO only once. Twenty-four individuals per species will be used.

Within each trial, I will measure responses of an individual to three phases (~ 6 min): (1<sup>st</sup>) visual search (no FALCO around), (2<sup>nd</sup>) FALCO detection, and (3<sup>rd</sup>) visual tracking of the FALCO. In the visual search phase, I will record visual search for 3 min and estimate head movement rates while the animal is in a head-up body posture. In the visual detection phase, I will record whether the FALCO is detected (1/0 response) based on various behaviors associated with changes in body posture and head orientation previously used in the literature (criteria in Tisdale & Fernández-Juricic 2009). Probability of predator detection will be estimated with a generalized linear model for each approach type and each species. In the visual tracking phase, I will score head movements to determine if the test subject follows the FALCO when the deviation of the head is less than 15 degrees from the direction of the FALCO within 1 sec (Voss & Bischof 2009) using Graphclick as described in Aim 2. Top-view projections of the fovea to estimate head orientation relative to the FALCO will be established for each species as explained in Aim 2. I will then estimate head movement rates and their intervals. I will control for food satiation levels (depending on species body mass) and light intensity and spectra to ensure that light conditions are similar to open and closed habitats and across trials.

**Aim 4: To assess how the inter-specific variability in the degree of retinal specialization, motion detection, visual acuity, and size of the blind area affects the gathering of predator information through visual search, visual detection, and visual tracking in visual conditions simulating closed and open habitats.** The outcome will be the identification of strategies of information gathering that favor predator detection under different visual conditions.

I will use path analysis, which is a special type of structural equation modeling (Keith 2006). This approach will allow me to determine the relative role of *both* the independent and combined effects of the four visual properties in antipredator behavior as well as the pathways of the association between vision and behavior (Fig. 6). The sampling unit will be each of the species studied. Habitat type (open, closed) will be included as the exogenous predictor (i.e., variable with no causal arrows pointing to it; Fig. 6). I will include degree of retinal specialization, double cone distribution, double cone density, visual acuity, size of blind area, and visual search as endogenous mediators (i.e., variables with both incoming and outgoing causal arrows; Fig. 6). Predator detection probability and visual tracking will be endogenous dependent variables (i.e., variables with only incoming causal arrows; Fig. 6). The sign of the relationships between visual properties and antipredator behavior follow the predictions formulated in the *Hypotheses, predictions, and preliminary information* section (Fig. 6). Additional relationships are described as follows. First, an increase in visual search through higher rates of eye and head movements is expected to increase the probabilities of predator detection, and the ability to visually track predators (Fig. 6). Second,

I will assess the correlations between the four visual properties studied; the significant ones (e.g., sensory trade-offs) will be included in the model. Third, the null expectation is that after an individual detects a predator, it will engage in visual tracking irrespective of the probabilities of detecting it in the first place; hence the lack of a path between these two variables (Fig. 6).

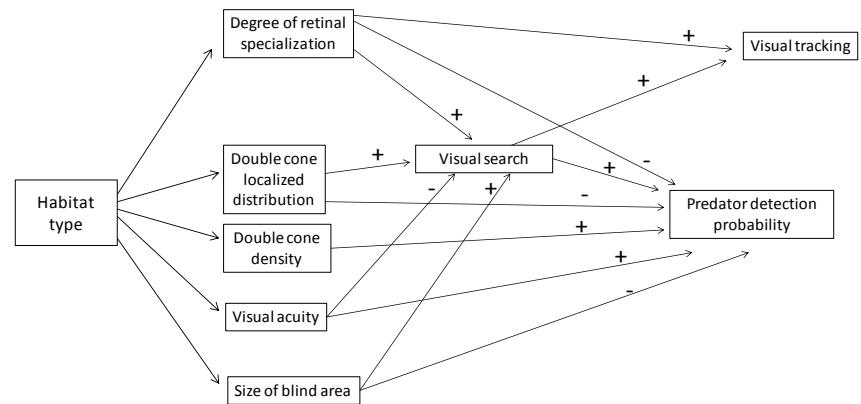


Fig. 6. Path analysis model. Arrows represent influences from presumed cause to presumed effect.

The path analysis will estimate the standardized direct, indirect, and total effects of the predetermined paths (Fig. 6), which will allow me to establish (a) the relationship between visual properties and antipredator behavior, and thus the strategies of information gathering in species with different sensory systems, and (b) the relative role of the different visual properties in accounting for predator detection under the two visual conditions simulating closed (i.e., short exposure times) and open (i.e., long exposure times) habitat types. The results of the lab (Aim#2) and semi-natural (Aim#3) experiments are complementary due to the different conditions in which they will be conducted. This can actually strengthen the conclusions of the present study by assessing antipredator behavior in conditions that will reveal first the mechanisms of visual information gathering in the lab and second the responses of individuals using those mechanisms in a more ecologically relevant scenario. Therefore, I will run separate path analyses for the lab and the semi-natural experiments. For all these analyses, I will use (1) species as independent data points, and (2) independent contrasts (see also Shine 1996). Raw species data potentially violate the statistical assumption of independence due to phylogenetic relatedness (Felsenstein 1985). I will use phylogenetic comparative methods to estimate independent contrasts (Felsenstein 1985) and determine the level of phylogenetic signal in the data following Blomberg et al. (2003). Independent contrasts will be calculated using two avian phylogenies [(1) based on Ericson et al. 2005, Jonsson & Fjeldsa 2006, Lüpold et al. 2009; and (2) based on gene sequencing data from GenBank: <http://www.ncbi.nlm.nih.gov/genbank/>), which will be tested for their statistical adequacy using the PDAP module of Mesquite (Maddison and Maddison 2008). The phylogenetic trees built for these analyses are available at: <http://estebanfj.bio.purdue.edu/vis&vig.html>. I will test the significance of different effects using two methods: bootstrap estimation and Baron and Kenny criteria. The goodness of fit of the path analysis model will be estimated with the Comparative Fit Index (Bollen 1989).

Besides testing the predictions already proposed, I will use the data to address other related questions in separate papers. (1) Have avian visual properties co-evolved to form different types of visual systems (e.g., species with deep foveae and greater degree of eye movement)? (2) How does vigilance behavior affect predator detection? (3) Is there a common mechanism of lateral visual fixation in species with different phylogeny, foraging micro-habitat, and visual system configuration?

**Timeline.** I will complete this project in three years. All the physiological and behavioral techniques proposed are already in place in my lab, with the exception of eye tracking, which will be developed in about 3 months. In the first two years, the general approach will be to capture individuals from different species, have them go through the behavioral tests (lab and then field), estimate the blind areas, and finally measure the visual properties for a subset of individuals (the rest will be released). My students and I have followed this approach successfully while gathering preliminary information for this proposal. We can obtain all the visual physiology parameters proposed for up to 8 individual birds per week, which means that we can potentially complete all the physiological sampling in 4 months (112 individuals from 14 species). We can run 6-10 behavioral trials a day in lab or semi-natural conditions, which means that we

can complete Aim 2 experiments in 21 – 35 days (210 trials with 15 individuals from each species) and Aim 3 experiments in 34 – 56 days (336 trials with 24 individuals from each species). In the second year, we will begin data analysis and presentations in scientific meetings. Publications will be submitted in the second and third years.

**Significance of the project.** This project will determine how key visual properties play a role in vigilance behavior and predator detection, and whether these two behavioral parameters are associated, as assumed by antipredator behavior theory (Pulliam 1973, Lima 1990, McNamara & Houston 1992). More importantly, this project will generate novel hypotheses about the mechanisms of information gathering in species with different visual systems and the combination of visual properties that increases predator detection in environments with different visual challenges. For instance, a high degree of retinal specialization associated with high acuity and directionality in visual performance may be a better strategy in an open habitat in which the detection of predators can be limited by the direction and distance at which the predator begins the attack. This can challenge the tenet of sensory asymmetry in predator-prey interactions (i.e., prey have good visual performance from any direction; Cronin 2005), as some prey may actually have sensory specializations to detect predators with directionality. Results will also have important implications for other aspects of behavioral predator-prey interactions. First, this study will provide a novel way of studying ‘perceived predation risk’, usually assessed behaviorally (Lima & Steury 2005, Whittingham et al. 2006, Schmidt et al. 2008, Rodriguez-Prieto et al. 2009), by considering how prey perceive risk through their own sensory cues. Second, this project will allow us to re-examine the trade-off between foraging and vigilance. Theory assumes that while animals are in vigilance postures (body head-up) they gather high quality information, but quality decreases during foraging (body head-down, Fernández-Juricic et al. 2004a). A novel understanding of visual information gathering strategies can be used to develop more realistic models and empirical tests of vigilance behavior in different body postures. Third, the outcome of this project will allow us to measure vigilance behavior at a finer scale through eye and head movement behavior (Jones et al. 2007a, 2009, Gall & Fernández-Juricic 2010) in species with different visual systems instead of the coarse indicator provided by the time or rate the animal spends in head-up postures. This will have applications to other fields (e.g., sexual selection, evolution of social behavior, cognitive ecology) because I will establish the visual strategies (eye/head movements) birds use to look at visual targets.

The findings of this project will be useful not only for predator-prey interactions, but also for other models in which predator detection probability plays a major role, such as, attention costs, mimicry, crypsis, optimal foraging, habitat selection, etc. (Dukas 1998, Ruxton et al. 2004, Stephens et al. 2007, Tosh & Ruxton 2010). By developing new knowledge on the anatomical and physiological processes underlying visual information gathering across taxa, the findings will be relevant to sensory ecology and comparative neurobiology. For instance, I am a member of a National Evolutionary Synthesis Center (NESCent) working group “Evolutionary Shifts in Vertebrate Visual Ecology and Visual System Morphology”. The comparative information generated in this project can be used by this working group to answer fundamental questions on the evolution of vision across vertebrates. This project will also introduce a novel sensory dimension to understand the evolution of antipredator strategies, and in particular how sensory systems and behavioral strategies can co-evolve to facilitate the gathering of different types of information (e.g., Smolka & Hemmi 2009). Overall, a better understanding of the association between sensory systems and behavior is critical to account for some of the mechanisms underlying animal communication, sexual selection, and speciation (Dangles et al. 2009, Martins 2010).